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ORIGINAL ARTICLE

Environmental drivers influencing stonefly assemblages along a longitudinal gradient in karst lotic habitats

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ABSTRACT

Stoneflies are among the most sensitive aquatic insect taxa and therefore arguably the best indicator of the excellent, *i.e.* pristine, ecological status of surface streams. Karst habitats are one of the most exciting freshwater habitats in terms of biological-geological interplay. They, in turn, support a biodiversity far superior to surrounding freshwater habitats and hence these habitats are designated as biodiversity hotspots. Our study deals with both of these crucial ecological players. We studied stonefly assemblages, their microhabitat preferences and emergence patterns along a karst oligotrophic hydrosystem. The sampling was conducted monthly from March 2007 to December 2008 using pyramid-type emergence traps set in various habitats and associated microhabitats (*e.g.* springs, rivers, streams, tufa barriers×moss, angiosperm, cobble, sand, silt substrates). Favorable environmental conditions, such as a wide range of karst habitat types with low water temperature and high oxygen concentration, resulted in high stonefly species richness (31 recorded species). Water temperature and pH had the highest influence on stonefly assemblages. Species richness and diversity decreased in a downstream direction. We recorded a longitudinal shift from crenal-epirhithral to epirhithral-metarhithral assemblages with some hyporhithral and potamal elements. Upstream sites were dominated by shredders, while downstream sites had a higher proportion of gatherers-collectors. Several species showed a significant preference for a specific microhabitat type in accordance with their feeding strategies and food availability. The majority of recorded species exhibited univoltine life cycles slow or fast.

Key words: Environmental relations; microhabitat preferences; trophic structure; longitudinal distribution; phenology.

Contributions: MI, MV, designed the research and analysed the data; MV, AR, wrote the paper; AR, IS, AP, MM, identified the specimens; MI, MM, ZM, collected the samples; MI, AR, sorted the samples; ZM, coordinated the project. All authors edited the drafts and approved the final version of the manuscript.

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INTRODUCTION

Many physical and chemical characteristics of the environment directly affect the distribution, abundance and behaviour of individual organisms and their populations. The "key-factors" influencing aquatic insects, including stoneflies, are water temperature, oxygen content, current-substrate relationships, and nutrient composition and availability (Ward and Stanford, 1982; Lamberti and Moore, 1984; Giller and Malmqvist 1998; Moog, 2002). Stoneflies (Plecoptera) inhabit a wide range of water qualities which is why they are widely used as bio-indicators of the health of freshwater ecosystems (Lenat, 1993; Walsh *et al*., 2007; Heino *et al*., 2009). Nevertheless, they were recognized as one of the most sensitive groups of aquatic invertebrates, occurring mainly in pristine habitats with high water quality (Hynes, 1976; Fochetti and Tierno de Figueroa, 2008; Stewart and Stark, 2008). Most nymphs live mainly in cold, well-oxygenated running waters, although some species have also been recorded from lakes (Lillehammer, 1978; Donald and Anderson, 1980; Saettem and Brittain, 1985; Fochetti and Tierno de Figueroa, 2008; DeWalt *et al.*, 2012). Moreover, many species preferably occur in a specific microhabitat, which is related to substrate type, current velocity, hydrological and thermal regime, species' feeding habits and availability of food resources (Cummins and Klug, 1979; Graf *et al*., 2009). However, comprehensive data about stonefly microhabitat preferences are so far known for only 18% of the European species, the need for more study is clear (see in Graf *et al*., 2009, 2017).

The final stage of many aquatic insects' life cycle is characterized by the transition from the aquatic larvae to the terrestrial adults, *i.e.* emergence (Davies, 1984). Stoneflies are one of the most important components of benthic macroinvertebrate communities in the lotic habitats which also undergo emergence (Corbet, 1964; Brittain, 1990). These hemimetabolous insects generally have very specific life cycles and flight periods with a tendency to emerge at specific time every year. Most often, their emergence periods are synchronous and short, with different species emerging in temporal succession (Hynes, 1976; Zwick, 2011). Although many environmental factors influence emergence of aquatic insects, water temperature and photoperiod have been recognized as the most important for stonefly emergence (Hynes, 1976; Flannagan and Cobb, 1991; DeWalt and Stewart, 1995; Zwick, 2011; Ivković *et al*., 2014; 2015).

Studies focusing on ecology and emergence patterns of the Central European stoneflies have increased in the last decade (Lock and Goethals, 2008; Graf *et al*., 2009; 2017; Zwick, 2011; Beracko *et al.,* 2016), yet studies in the area of Southern Europe have remained rather scarce and mainly focused on checklists (Kaćanski, 1976; Sivec, 2001; Popijač and Sivec, 2009, 2010, 2011a, 2011b; Petrović *et al*., 2014). Therefore, our study was conducted in an oligotrophic hydrosystem located in the Dinaric karst area, the largest continuous karst landscape in Europe, extending over approximately 60,000 km^2 (Mihevc *et al*., 2010). This complex karst landscape is formed from hydrological and geological characteristics working on water soluble rock over long time periods. Specific geology and hydrology of these habitats, including vast array of available microhabitats, resulted in high level of speciation and endemism, which is why karst habitats were recognized as biodiversity hotspots (Bonacci, 2009; Ivković and Plant, 2015; Previšić *et al*., 2014). Nevertheless, ecology of their biota, including stoneflies, is still highly understudied (Previšić *et al.,* 2007; Ivković *et al*., 2012, 2014; Šemnički *et al.,* 2012; Čmrlec *et al*., 2013; Vilenica *et al.,* 2017a).

Unfortunately, these habitats are highly endangered by increasing anthropogenic impact (Obelić *et al*., 2005; Freyhof, 2012). Humans have benefited from karst freshwater habitats for ages, as they represent an important source of drinking water. In modern times these hydrosystems are heavily used for recreation, irrigation, and industrial purposes, putting their unique fauna and flora at risk. Therefore, it is of main importance to protect these habitats and their biota. The first step to achieving this is collecting the required ecological data.

We therefore aim to fill the existing gap in knowledge about the ecological traits and emergence patterns of European stoneflies, with a special emphasis on karst lotic habitats. Our main goals were to determine: i) the composition and structure of stonefly assemblages and their spatial distribution; ii) the environmental factors important for structuring stonefly assemblages; iii) stonefly preferences for microhabitat types (*i.e.* substrate and water velocity); and iv) the temporal distribution and emergence patterns of stoneflies along an oligotrophic karst hydrosystem.

METHODS

Study area

The study was conducted in the Plitvice Lakes National Park, a 295 km^2 forest reserve located in the karst region of the north-western Dinaric Mountains, in mountainous part of Croatia. Sixteen fluvial lakes divided by numerous tufa barriers form an approximately 8.2 km long barrage system. The lakes are characterized by low organic solute concentrations, supersaturation with calcium salts, pH >8 and the presence of algae and mosses mediating tufa barrier formation (Srdoč *et al.,* 1985; Stilinović and Božičević, 1998). The main surface-water supplier for the lakes is the Matica River, formed by the merging of two small mountainous rivers, Bijela rijeka and Crna rijeka. The area of the Plitvice Lakes NP has a temperate humid climate with a warm summer but is also influenced by a boreal climate (Köppen climate classification, Šegota and Filipčić, 2003).

The study encompassed nine sampling sites belonging to the following habitat types (for details see Vilenica *et al*., 2017a, 2017b):

1. Upper lotic habitats at the beginning of the barrage-lake system represented by:
   a) rheocrene springs of small mountain rivers: Bijela rijeka River Spring (BS) and Crna rijeka River Spring (CS)
   b) downstream sections of small mountain rivers: upper reaches of the Bijela rijeka River (BUR), upper reaches of the Crna rijeka River (CUR)
2. Tufa barriers: Labudovac (LB), Kozjak-Milanovac (KM) and Novakovića Brod (NOB)
3. Lower lotic habitats at the end of the barrage-lake system represented by:
   a) canyon type mountain streams, the Plitvica Stream (PS)
   b) mid-altitude lowland river, the Korana River (KR) (Fig. 1, Tab. 1).

Sampling and experimental protocol

Adult stoneflies were collected monthly from March 2007 to December 2008 using pyramid type emergence traps. Each trap was a four-sided, 50 cm tall pyramid, with a base of 45×45 cm. Traps were fastened to the streambed in a way that allowed the free movement of larvae in and out of the sampling area. The side frames of the traps were covered with 1 mm mesh netting. At the top of each trap collecting containers were placed and filled with preservative (2% formaldehyde with detergent). Six emergence traps were installed at each study site covering all major microhabitats representing at least 5% coverage. At each sampling point (each emergence trap), the substrate categories present were defined based on Wentworth scale (Wentworth, 1922). The containers were emptied monthly and samples were preserved in 80% ethanol. Specimens were identified using Kaćanski and Zwick (1970), Kis (1974), Krno (1985), Zwick and Mendl (1989), Ravizza and Vinçon (1998), Ravizza (2002), Graf and Schmidt-Kloiber (2003), Zwick (2004) and Murányi (2011).

Physical and chemical water properties were measured at each study site, once each month, when the containers with insects were emptied. Oxygen concentration and saturation, water temperature, pH and conductivity were measured using WTW probes (WTW Oxi 330/SET, WTW pH 330 and WTW LF 330), while alkalinity concentration was measured by titration with 0.1 M HCl with methyl orange used as the titration indicator. Additionally, at each study site, a HOBO Pendant Temperature Data Logger (#Part UA-001-XX, Bourne, MA, USA) measured water temperature every two hours throughout the whole study period. Water velocity was measured by P-670-M series instrument (Dostmann electronic) once each month at each sampling point (*i.e.* each trap). The Meteorological and Hydrological Institute of Croatia provided us with stream discharge data.

Data analyses

The analyses were performed on monthly samples over a two-year period. The Shapiro-Wilk normality test was performed for all data, statistical tests chosen according to the normality of data. All species data were log transformed prior to analyses.

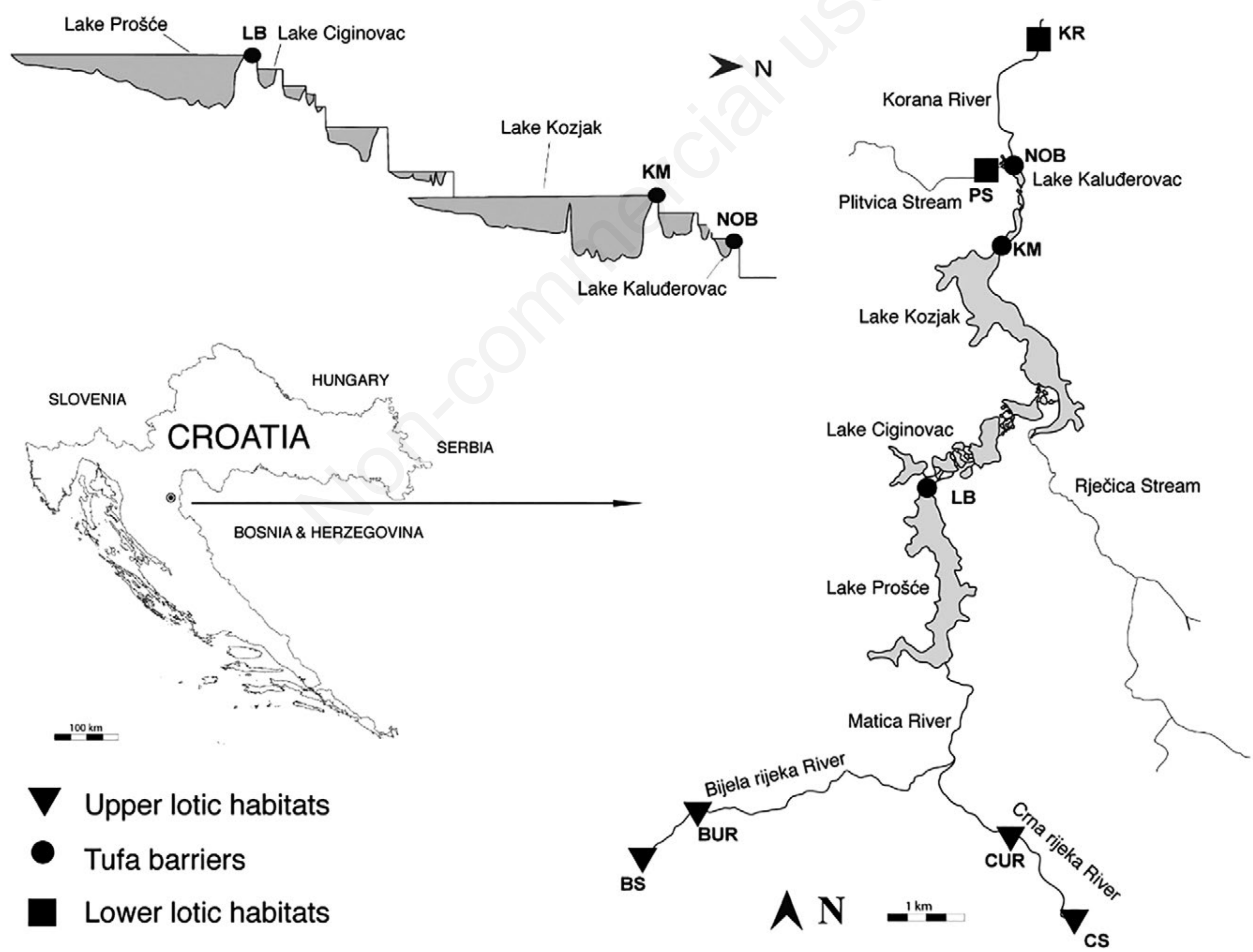

Fig. 1. Locations of sampling sites in the Plitvice Lakes National Park, Croatia. BS, Bijela rijeka River spring; BUR, Bijela rijeka River upper reaches; CS, Crna rijeka River spring; CUR, Crna rijeka River upper reaches; LB, tufa barrier Labudovac; KM, tufa barrier Kozjak-Milanovac; NOB, tufa barrier Novakovića Brod; PS, Plitvica Stream; KR, Korana River.

Tab. 1. Characteristics of the studied sites in the Plitvice Lakes NP.

Site		BS	BUR	CS	CUR	LB	KM	NOB	PS	KR
Latitude		N 44°50"05'	N 44°50"04'	N 44°50"14'	N 44°50"10'	N 44°52"17'	N 44°53"39'	N 44°54"07'	N 44°54"07'	N 44°55"33'
Longitude		E 15°33"43'	E 15°33"33'	E 15°36"28'	E 15°36"30'	E 15°35"59'	E 15°36"32'	E 15°36"38'	E 15°36"27'	E 15°37"09'
Altitude (m)		720	716	677	670	630	546	504	556	390
Substrate		Cobbles and sand, angiosperms, mosses	Cobbles and sand, angiosperms, mosses	Cobbles and sand, angiosperms, mosses	Cobbles and sand, angiosperms, mosses	Cobbles, mosses on tufa, tufa with detritus	Cobbles, mosses on tufa, tufa with detritus, silt	Cobbles, mosses on tufa, tufa with detritus, silt	Cobbles, mosses on tufa, tufa with detritus, silt	Cobbles, mosses on tufa, tufa with detritus, silt
Water temperature (°C)	min	7.3	7.2	7.7	7.1	2.5	3.1	3.3	3.2	1.7
	max	7.8	9.9	8.2	9.7	20.5	22.9	22.9	15.4	19.8
O_2 (mg L^{-1})	min	7.6	8.2	8.3	7.9	6.7	8.7	8.4	8.7	9
	max	11.8	11.8	11.7	12.5	12.3	12	12.4	13	14.1
O_2 (%)	min	65.2	71.2	87	68.8	59.7	72	77.3	75.7	79.6
	max	101.8	106.6	105.7	115.9	139.2	113.6	117.1	122.5	121
pH	min	6.9	7.5	7.4	7.7	6.8	6.9	8.2	6.8	6.8
	max	7.8	8.4	8.2	8.6	8.7	8.4	8.7	8.9	8.7
Conductivity (µS cm^{-1})	min	463	472	405	403	366	354	334	409	321
	max	505	498	424	426	426	443	387	444	385
Alkalinity (mg L^{-1} $CaCO_3$)	min	235	230	210	210	210	200	185	225	180
	max	295	295	260	290	260	220	230	280	215

BS, Bijela rijeka River spring; BUR, Bijela rijeka River upper reaches; CS, Crna rijeka River spring; CUR, Crna rijeka River upper reaches; LB, tufa barrier Labudovac; KM, tufa barrier Kozjak-Milanovac; NOB, tufa barrier Novakovića Brod; PS, Plitvica Stream; KR, Korana River.

Non-metric multidimensional scaling analysis (NMDS) based on the Bray-Curtis similarity index was used to detect similarity of stonefly assemblages between the studied sites. In order to estimate differences in composition and diversity of stonefly assemblages between the studied sites, Shannon diversity index (Shannon, 1948) was calculated for each site. The latter two analyses were performed in Primer 5.2.9. software package (Clarke and Gorley, 2006). The composition of stonefly assemblages in terms of longitudinal distribution and trophic structure at sampling sites was based on the classification given by Graf *et al.* (2009, 2017). Canonical correspondence analysis (CCA) was used to ordinate stonefly occurrence in respect to environmental variables. It was performed using data for 38 taxa (rare taxa were downweighed) and six environmental variables. The Monte Carlo permutation test with 999 permutations was used to test the statistical significance of the relationship between all taxa and all variables. The CCA analysis was performed using CANOCO for Windows (ver. 4.02) (Ter Braak and Šmilauer, 1998). In order to determine the preferences of each individual species for a specific microhabitat, *i.e.* substrate type and water velocity, the Kruskal-Wallis H test (followed by Multiple comparisons *post-hoc* test) and Spearman's rank correlation coefficient were used, respectively. These analyses were performed using Statistica 10.0 (Statsoft, 2010).

RESULTS

Environmental factors

Overall, tufa barriers had higher mean and maximum water temperatures and lower mean oxygen concentration compared to other habitat types. Upper lotic habitats had a slightly higher mean alkalinity and conductivity, and lower values of pH compared to tufa barriers and lower lotic habitats (Tab. 1). Other significant differences between habitat types are discussed in the study by Vilenica *et al.* (2017b).

Differences in water temperature and discharge between the two studied years were also recorded. Water temperatures were higher in spring 2007 (excluding springs and spring headwaters which were characterized by stable water temperatures throughout the year) than in spring 2008. Moreover, water temperatures in autumn 2007 were lower than in autumn 2008 (Tab. 2). A higher mean water discharge was recorded in 2008 compared to 2007 (Fig. 2).

Stonefly assemblages

A total of 14,155 individuals belonging to 31 species, (plus five genera not identified to the species level), contained within four families were collected. Taxa richness and abundance at different habitats varied considerably between the two studied years. In upper lotic habitats, more taxa were collected in 2008, while fewer were collected from tufa barriers and lower lotic habitats during the same year compared to 2007. Furthermore, stonefly abundance at the two tufa barriers (LB, NOB) and the Plitvica Stream (PS) was higher in 2007 compared to 2008, while the opposite was recorded for the Bijela rijeka River (BS, BUR), the Korana River (KR) and one tufa barrier (KM). Abundances at the Crna rijeka River (CS, CUR) were comparable between the two years (Tab. 3).

Springs (BS, CS) had both a lower taxa richness and a lower abundance compared to other study sites. Stonefly abundance was highest at tufa barriers and at the Korana River, but taxa richness was low compared to other sites. However, the Shannon diversity index ranged from 2.05 to 2.91, and the most diverse assemblages were recorded at the upper reaches of the Bijela rijeka (BUR) and Crna rijeka (CUR) Rivers. The two tufa barriers (KM, LB) supported the least diverse assemblages (Tab. 3).

Differences in species composition at different habitat types were also observed. For instance, *Protonemura auberti* Illies, 1954 was recorded only at upper lotic habitats, while *Amphinemura triangularis* (Ris, 1902), *P. intricata* (Ris, 1902), *Leuctra albida* Kempny, 1899 and *L. fusca* (Linnaeus, 1758) preferred lower elevation lotic habitats. Furthermore, some species were recorded only during one of the two studied years (*e.g. L. pusilla* Krno, 1985 only in 2007; *L. handlirschi* Kempny, 1898, *L. hippopus* Kempny, 1899, *L. inermis* Kempny, 1899, *L. prima* Kempny, 1899, *Isoperla rivulorum* (Pictet, 1841) and *Perlodes* cf. *intricatus* Pictet, 1841 only in 2008) (Tab. 3).

The NMDS analysis demonstrated that stonefly assemblages grouped based on habitat type (Fig. 3): sampling points located in upper lotic habitats [including those at springs (BS, CS) and upper reaches of the small mountainous rivers (BUR, CUR)] formed one cluster while sampling points located at tufa barriers (LB, KM, NOB) and lower lotic habitats (PS, KR) formed another

Tab. 2. Fluctuations of the water temperature during the spring and autumn 2007 and 2008 in the Plitvice Lakes NP.

Study site			BS	BUR	CS	CUR	LB	KM	NOB	PS	KR
Water temperature (°C)	2007	April	7.6	7.6	7.7	7.7	10.3	10.3	10.5	9.8	10.7
		November	7.6	7.5	7.7	7.5	6.3	8.3	8.1	6.0	7.2
	2008	April	7.6	7.5	7.7	7.6	8.0	8.5	8.6	8.6	7.9
		November	7.6	7.6	7.7	7.8	7.0	8.9	12.0	7.3	9.6

BS, Bijela rijeka River spring; BUR, Bijela rijeka River upper reaches; CS, Crna rijeka River spring; CUR, Crna rijeka River upper reaches; LB, tufa barrier Labudovac; KM, tufa barrier Kozjak-Milanovac; NOB, tufa barrier Novakovića Brod; PS, Plitvica Stream; KR, Korana River.

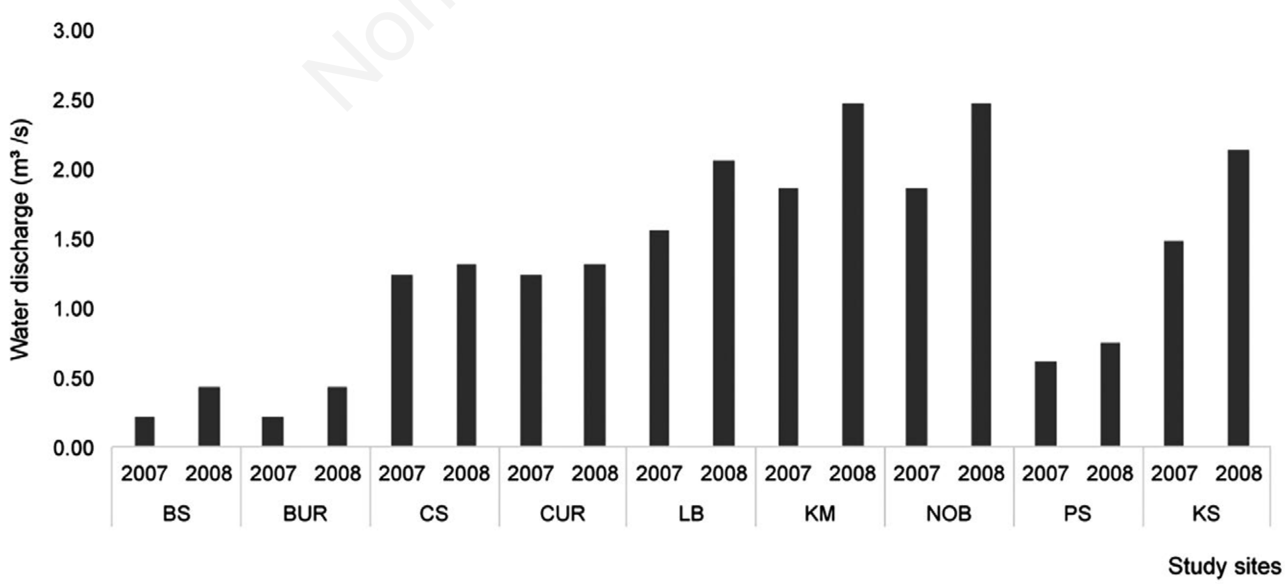

Fig. 2. Average water discharge in the Plitvice Lakes NP in 2007 and 2008. Abbreviations of the study site names as in Fig. 1.

Tab. 3. Distribution and abundance of stoneflies in the Plitvice Lakes NP based on emergence method collection. Taxa codes are those used in CCA analysis.

Taxa	Taxa code	BS		BUR		CS		CUR		LB		KM		NOB		PS		KR	
		2007	2008	2007	2008	2007	2008	2007	2008	2007	2008	2007	2008	2007	2008	2007	2008	2007	2008
TAENIOPTERYGIDAE																			
Brachyptera monilicornis (Pictet, 1841)	*1*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	41
Brachyptera risi (Morton, 1896)	*2*	0	1	0	7	0	0	0	0	0	0	0	0	0	0	13	5	20	26
Brachyptera tristis (Klapálek, 1901)	*3*	1	10	0	1	2	4	0	0	0	0	0	0	0	0	0	0	0	0
Taeniopteryx hubaulti Aubert, 1946	*4*	1	1	22	17	31	5	14	23	0	0	0	0	0	0	0	0	0	3
LEUCTRIDAE																			
Leuctra albida Kempny, 1899	*5*	1	1	0	31	0	0	6	0	235	369	4	20	0	16	41	26	0	0
Leuctra cingulata Kempny, 1899	*6*	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Leuctra fusca (Linnaeus 1758)	*7*	0	0	0	0	0	0	0	0	270	371	8	7	2	19	4	22	2	24
Leuctra handlirschi Kampny, 1898	*8*	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0
Leuctra hippopus Kampny, 1899	*9*	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
Leuctra inermis Kempny, 1899	*10*	0	0	0	76	0	71	0	86	0	0	0	0	0	0	0	0	0	0
Leuctra major Brinck, 1949	*11*	0	0	0	0	0	0	0	0	0	0	5	0	8	3	0	0	0	0
Leuctra nigra (Olivier, 1811)	*12*	1	2	10	208	0	0	24	84	8	12	28	8	0	0	6	6	0	0
Leuctra prima Kempny, 1899	*13*	0	1	0	13	0	0	0	11	0	0	0	0	0	0	0	0	0	0
Leuctra cf. *pusilla* Krno, 1985	*14*	0	0	28	0	28	0	73	0	0	0	0	0	0	0	0	0	0	0
Leuctra non det.	*15*	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0
NEMOURIDAE																			
Amphinemura triangularis (Ris, 1902)	*16*	0	0	0	0	0	0	0	0	315	34	23	2	873	317	335	68	327	2
Nemoura avicularis Morton, 1894	*17*	0	0	0	0	0	0	0	0	10	0	0	0	2	0	7	2	6	0
Nemoura cinerea (Retzius, 1783)	*18*	0	0	1	11	0	0	0	0	40	40	376	946	15	12	91	11	31	6
Nemoura flexuosa Aubert, 1949	*19*	0	0	0	0	0	0	0	5	0	0	0	0	0	0	6	2	0	0
Nemoura marginata Pictet, 1835	*20*	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nemoura minima Aubert, 1946	*21*	0	0	3	0	0	0	10	10	0	0	0	0	0	0	0	0	0	0
Nemoura non det.	*22*	0	0	0	1	1	0	0	0	0	0	0	0	2	0	2	1	0	0
Nemurella pictetii (Klapálek, 1900)	*23*	30	14	15	19	0	0	1	0	0	2	0	0	0	0	8	5	0	0
Protonemura auberti Illies, 1954	*24*	171	431	121	634	280	252	159	82	0	0	0	0	0	0	4	67	0	0
Protonemura intricata (Ris, 1902)	*25*	0	0	0	0	0	0	0	0	560	125	350	52	340	153	33	63	777	1528
Protonemura nitida (Pictet, 1836)	*26*	0	0	0	0	12	35	14	6	0	0	0	0	0	0	21	96	0	0
Protonemura praecox (Morton, 1894)	*27*	0	0	1	7	0	0	0	1	310	1	20	0	58	0	64	35	25	0
Protonemura non det.	*28*	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0
PERLODIDAE																			
Besdolus imhoffi (Pictet, 1841)	*29*	0	0	0	0	0	0	0	0	0	0	0	1	2	2	0	0	0	0
Isoperla inermis Kaćanski & Zwick, 1970	*30*	35	0	92	29	8	0	13	2	0	0	0	0	0	0	1	0	0	0
Isoperla cf. *lugens* (Klapálek, 1923)	*31*	3	0	40	57	16	0	8	2	0	0	0	0	0	0	149	89	2	0
Isoperla oxylepis (Despax, 1936)	*32*	0	0	0	0	0	0	0	0	0	0	0	0	5	11	0	0	11	44
Isoperla rivulorum (Pictet, 1841)	*33*	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0
Isoperla non det.	*34*	0	3	2	15	0	0	12	0	0	0	0	0	1	0	0	0	0	0
Perlodes cf. *intricatus* Pictet, 1841	*35*	0	0	0	0	0	1	0	10	0	0	0	0	0	0	0	0	0	0
Perlodes non det.	*36*	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0
Number of individuals		243	464	336	1130	378	370	338	339	1748	954	814	1036	1308	533	786	499	1205	1674
Number of taxa		8	9	12	18	8	7	12	16	8	8	8	7	11	8	17	16	10	8
Total number of taxa		11		20		11		21		9		9		12		18		11	
Shannon diversity index		2.12		2.82		2.22		2.91		2.10		2.05		2.30		2.74		2.27	

BS, Bijela rijeka River spring; BUR, Bijela rijeka River upper reaches; CS, Crna rijeka River spring; CUR, Crna rijeka River upper reaches; LB, tufa barrier Labudovac; KM, tufa barrier Kozjak-Milanovac; NOB, tufa barrier Novakovića Brod; PS, Plitvica Stream; KR, Korana River.

one. One sampling point located at a microhabitat on a mixture of sand and silt at tufa barrier NOB separated independently (Fig. 3).

The longitudinal distribution (Fig. 4a) varied among sites and showed a shift in species composition from assemblages dominated by crenal and epirhithral elements at upper lotic habitats to those dominated by epirhithral-metarhithral elements at tufa barriers and lower lotic habitats, where potamal elements also occurred.

The trophic structure was dominated by shredders at the upper lotic habitats, while scrapers and gatherers-collectors were equally represented (Fig. 4b). Tufa barriers and the Korana River were dominated by gatherers-collectors, while the Plitvica Stream was almost equally represented by shredders, scrapers and gatherers-collectors. Predators were poorly represented at all sites and almost completely absent from tufa barriers (an exception was NOB). The Bijela rijeka River and the Plitvica Stream displayed a slightly higher proportion of predators compared with other sites.

Environmental relations and microhabitat preferences of stoneflies

The results of the ordination of taxa and environmental data of the CCA are presented on the F1×F2 ordination plot (Fig. 5). The eigenvalues for the first two CCA axes were 0.69 and 0.22 and explained 70.8% of the taxa-environment relations. The Monte Carlo permutation test showed that the taxa-environment ordination was statistically significant (first axis: F-ratio=15.89, P=0.002; overall: trace=1.29, F=6.96, P=0.002) indicating that the stonefly assemblages were significantly related to the tested set of environmental variables. Axis 1 demonstrated that maximum water temperature (R=-0.97) and pH (R=-0.83) were the most important variables influencing species distributions. Axis 2 presented mean oxygen concentration (R=0.43) as being an important variable.

The Kruskal-Wallis H test and Multiple Comparisons *post hoc* test highlighted a significant difference between abundances of individuals at different substrates for *P. intricata* (H=18.25, df=3, N=48, P<0.001), *A. triangularis* (H=11.52, df=3, N=42, P<0.01) and *P. praecox* (Morton, 1894) (H=9.35, df=3, N=30, P<0.01). All three species preferred microhabitats with mosses. Spearman's rank correlation showed a weak but significant (P<0.05) positive correlation between water velocity and abundance of *P. intricata* (R=0.57), *P. praecox* (R=0.42) and *P. auberti* (R=0.37).

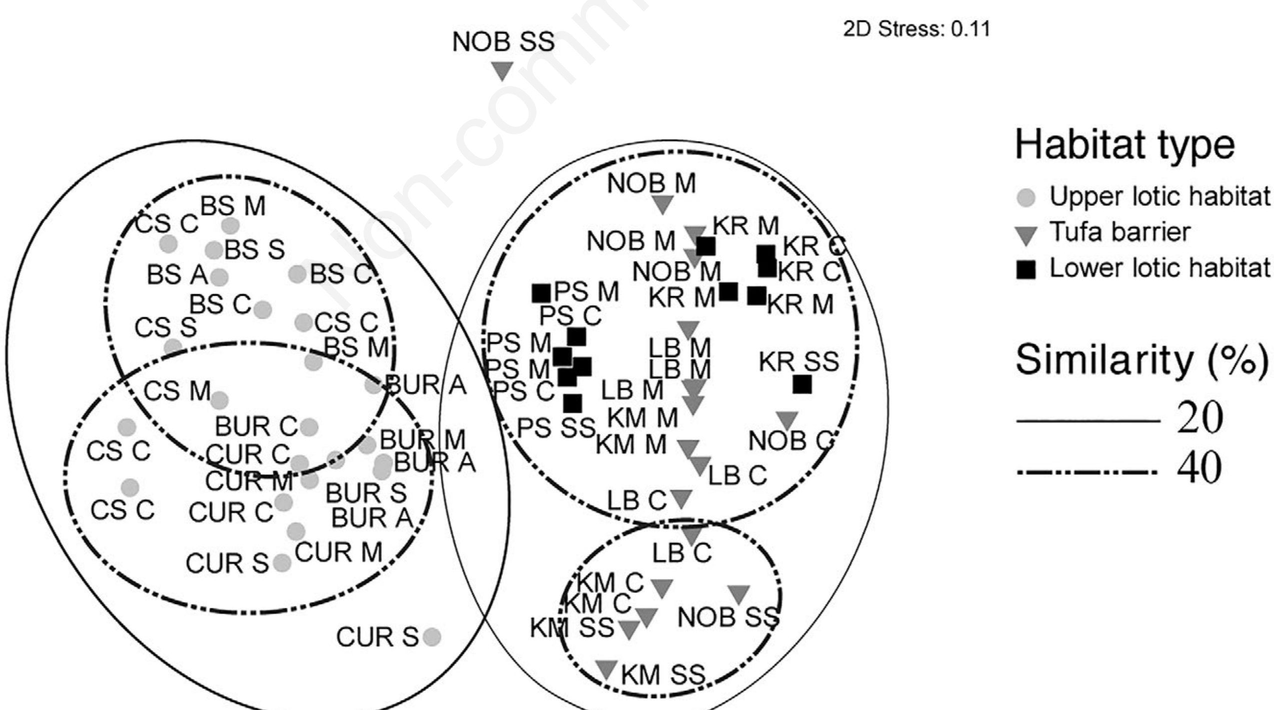

Fig. 3. Non-metric multidimensional scaling (NMDS) ordination of stonefly assemblages based on the Bray-Curtis similarity coefficient (group average linking) and their log transformed abundances based on a habitat type in the Plitvice Lakes NP. A, angiosperms; M, mosses; C, cobbles; S, sand; SS, sand and silt. Abbreviations of the study site names as in Fig. 1.

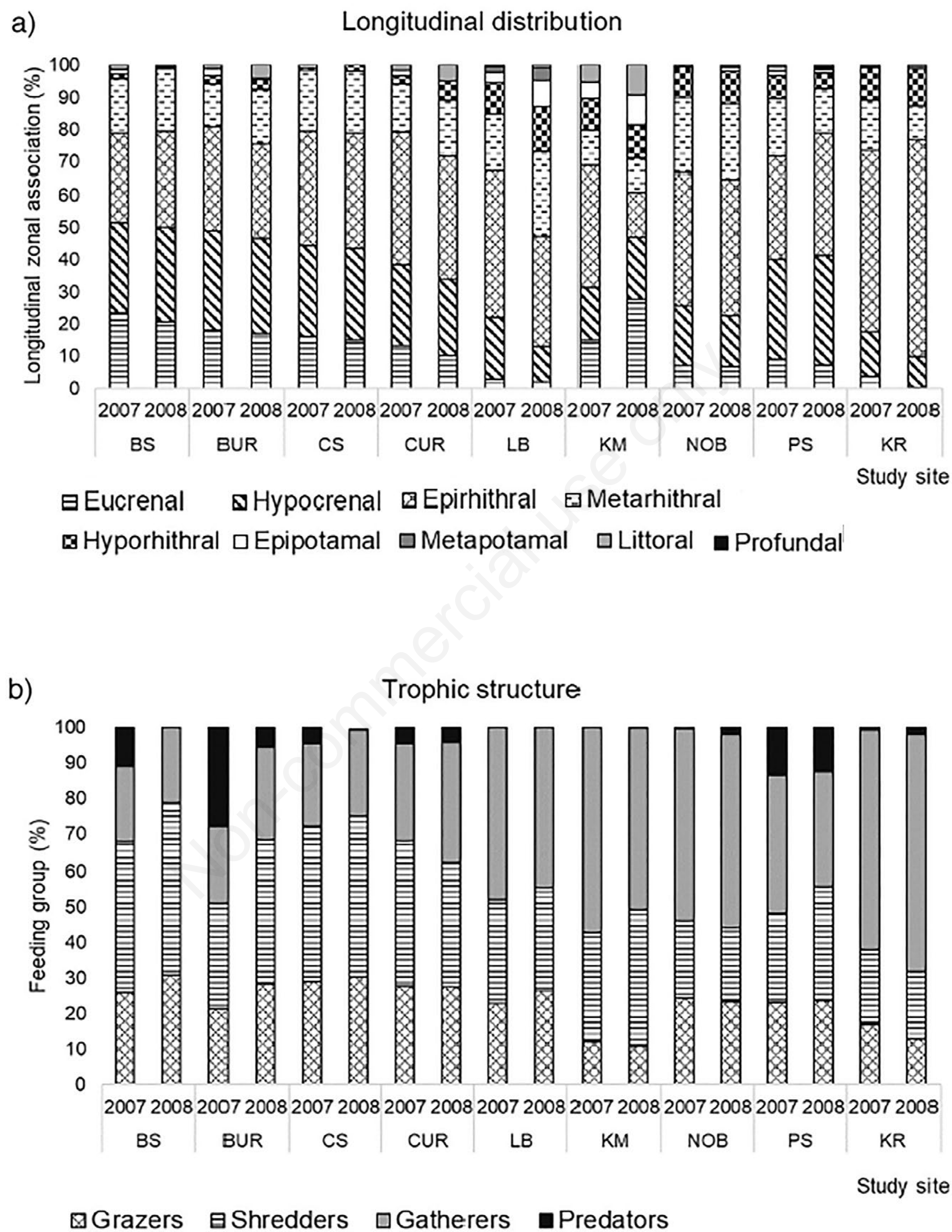

Fig. 4. a) Longitudinal zonal associations and b) Trophic structure of stonefly assemblages at study sites in the Plitvice Lakes NP. Abbreviations of the study site names as in Fig. 1.

Stonefly emergence patterns

The stonefly emergence patterns were comparable between the two studied years. Emergence occurred between February and November (Fig. 6). The emergence period was shorter in tufa barriers compared to other habitats (Fig. 7).

Emergence peaked in April and May with between 16 and 22 taxa and with the highest number of emerging individuals (Figs. 6 and 7). *Protonemura auberti* had the longest emergence periods, which lasted approximately from six to eight months. Within the two studied years, most of the analyzed taxa exhibited unimodal emergence patterns (Tab. 4). However, for *Nemurella pictetii* (Klápalek 1900), *L. nigra* and *L. albida* two flight periods per year were recorded at some sites (Tab. 4).

We also observed some differences in the beginning and duration of emergence periods between 2007 and 2008 (Tab. 4). For instance, the emergence of most taxa from the family Perlodidae started earlier in 2007 compared to 2008, whereas *L. nigra* (Olivier, 1811) emerged earlier in 2008 and its flight period during this year was longer than in 2007 (Tab. 4).

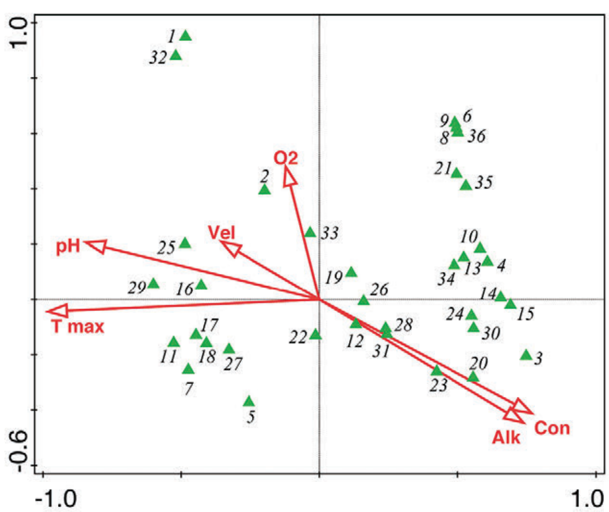

Fig. 5. F1 x F2 plane of canonical correspondence analysis (CCA) based on 38 stonefly taxa and six selected environmental variables. For the abbreviations of the species codes (green triangle symbols) see Tab. 3. Environmental variables (red arrow symbols): T max, maximum water temperature; pH, mean pH value; Vel, mean water velocity (m s^{-1}); O2, mean oxygen concentration (mg L^{-1}); Alk mean alkalinity (mg L^{-1} $CaCO_3$); Con, mean conductivity (µS cm^{-1}).

DISCUSSION

Stonefly assemblages and relationships with environmental variables and microhabitats

Species richness in this karst system is high given that it represents 34% of the Croatian total stonefly fauna (Popijač *et al*., 2017). Many species were cold stenotherms (*e.g. P. auberti*, *L. prima*, *L. pusilla*, *Taeniopteryx hubaulti*) (Graf *et al*., 2009, 2017), relating to favourable environmental conditions (*i.e.* low water temperature and high oxygen concentration; Hynes, 1976; Fochetti and Tierno de Figueroa, 2008; Zwick, 2011) and the wide range of suitable habitats (Riđanović and Božićević, 1996; Miliša *et al*., 2010). The differences in abundance and taxa richness between the two studied years could be attributed to the variability of environmental conditions, especially water temperature and discharge, as already shown in some other studies (Zwick, 2011; Ivković *et al.,* 2012, 2014; Vilenica *et al*., 2017a).

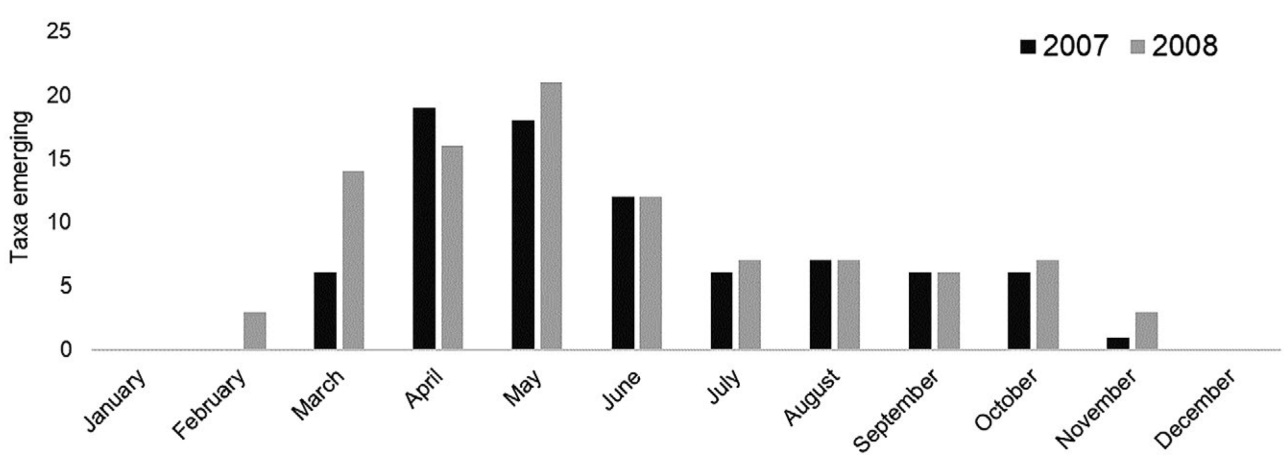

Fig. 6. Stonefly emergence periods in the area of the Plitvice Lakes NP, Croatia in 2007 and 2008.

As the majority of stonefly species prefer the headwaters of lotic habitats (Graf and Schmidt-Kloiber A, 2003; Graf *et al*., 2009, 2017), taxa richness generally decreased downstream as expected and supported by preliminary studies (Vannote *et al.,* 1980; Popijač and Sivec, 2009, 2011b). The exception was Plitvica Stream, which supported a higher taxa diversity due to its high microhabitat heterogeneity (Waringer, 1996; Wiberg-Larsen *et al*., 2000) and the availability of various food resources (Miliša *et al*., 2006; Špoljar *et al*., 2007; Vilenica *et al*., 2017a, 2017b). As expected for karst hydrosystem, the assemblage structure showed a downstream longitudinal shift from domination of crenal-epirhithral elements to domination of epirhithral-metarhithral with some hyporhithral and potamal elements. This longitudinal shift reflects a higher abundance of taxa as *P. auberti*, *N. pictetii* and *I. inermis* at upper lotic habitats and taxa such as *L. fusca* and *N. cinerea* towards the tufa barriers and lower lotic habitats (Graf *et al*., 2009, 2017). Therefore, in terms of longitudinal zonal associations of stonefly assemblages, these results are generally not in agreement with the predictions of the River Continuum Concept (Vannote *et al.,* 1980), which has already been observed for other aquatic insects of the same hydrosystem (Šemnički *et al*., 2012; Ivković *et al*., 2014; Vilenica *et al*., 2017a) and also for other karst rivers in the region (Habdija *et al*., 2002; Vilenica *et al*., 2016).

NMDS analysis confirmed the differences between stonefly assemblages upstream and downstream in the hydrosystem due to differences in physical and chemical water properties, microhabitat composition and food availability (see also in Vilenica *et al*., 2017a, 2017b). A microhabitat on a mixture of sand and silt at the tufa barrier Novakovića Brod separated independently due to the very low number of recorded individuals, as Plecoptera do not prefer such microhabitats (Hershey *et al*., 2010; Merten *et al*., 2014). The CCA analysis indicated that water temperature and pH patterns provide the best explanation for the distribution and composition of stonefly assemblages, *i.e*. stoneflies preferred habitats with lower water temperature and neutral pH. The composition of stonefly assemblages was clearly a consequence of the position of the habitat within the hydrosystem, which resulted in differences of physical and chemical factors as well as nutrient and energy sources at habitats located at different elevations. Similar patterns in distribution and influence of environmental factors were observed for other aquatic insects in the same hydrosystem, *i.e*. for caddisflies (Šemnički *et al*., 2012), dance flies (Ivković *et al*., 2012), blackflies (Ivković *et al*., 2014) and mayflies (Vilenica *et al*., 2017a, 2017b). Interestingly, higher abundances of the cold stenotherm *P. praecox* were recorded at the tufa barriers and lower lotic habitats. Even though the species was already

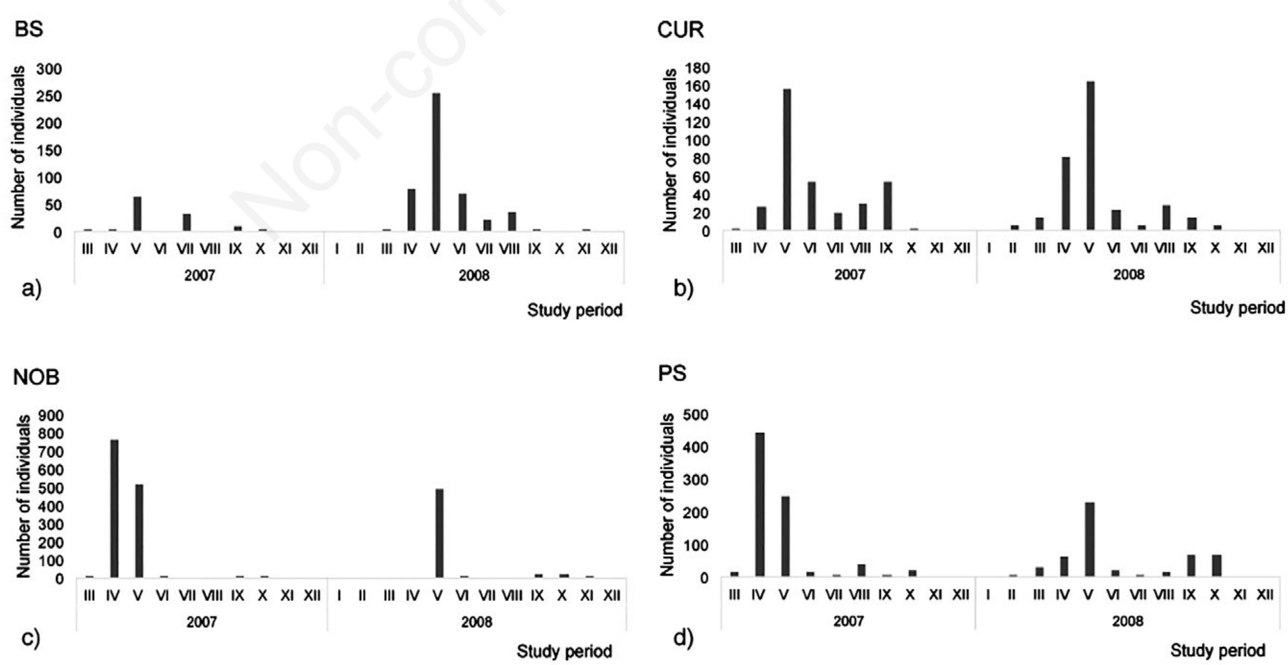

Fig. 7. Stonefly emergence periods in four habitat types in the area of the Plitvice Lakes NP, Croatia in 2007 and 2008. a) Spring of upper lotic habitat (Bijela rijeka River Spring), b) Upper reaches of upper lotic habitat (Upper reaches of the Crna rijeka River), c) Tufa barrier (tufa barrier Novakovića-Brod) and d) Lower lotic habitat (Plitvica Stream).

Tab. 4. Flight periods of stonefly species recorded in the Plitvice Lakes NP over a two-year period.

Taxa	2007												2008											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
TAENIOPTERYGIDAE																								
Brachyptera monilicornis (Pictet, 1841)				x										x	x									
Brachyptera risi (Morton, 1896)			x	x											x	x	x							
Brachyptera tristis (Klapálek, 1901)				x	x										x		x	x						
Taeniopteryx cf. *hubaulti* Aubert, 1946			x	x	x										x	x	x							
LEUCTRIDAE																								
Leuctra albida Kempny, 1899			x					x	x	x	x				x	x		x		x	x	x	x	
Leuctra cingulata Kempny, 1899																					x			
Leuctra fusca (Linnaeus, 1758)									x	x											x	x	x	
Leuctra handlirschi Kempny, 1898																	x			x				
Leuctra hippopus Kempny, 1899															x	x								
Leuctra inermis Kempny, 1899															x	x	x							
Leuctra major Brinck, 1949									x													x	x	
Leuctra nigra (Olivier, 1811)				x	x	x				x				x	x	x	x	x	x			x		
Leuctra prima Kempny, 1899														x	x									
Leuctra cf. *pusilla* Krno, 1985				x	x	x																		
Leuctra non det.															x	x								
NEMOURIDAE																								
Amphinemura triangularis (Ris, 1902)				x	x											x	x							
Nemoura avicularis Morton, 1894			x	x	x										x									
Nemoura cinerea (Retzius, 1783)				x	x	x		x									x	x						
Nemoura flexuosa Aubert, 1949				x												x	x							
Nemoura marginata Pictet, 1835					x											x								
Nemoura minima Aubert, 1946				x	x											x	x							
Nemoura non det.				x	x	x									x	x								
Nemurella pictetii (Klapálek, 1900)				x	x	x	x	x	x	x						x	x				x	x	x	
Protonemura auberti Illies, 1954			x	x	x	x	x	x	x	x					x	x	x	x	x	x	x	x		
Protonemura intricata (Ris, 1902)				x	x	x										x	x	x						
Protonemura nitida (Pictet, 1836)									x	x										x	x	x		
Protonemura praecox (Morton, 1894)			x	x											x	x	x							
Protonemura non det.				x													x							
PERLODIDAE																								
Besdolus imhoffi (Pictet, 1841)					x	x											x							
Isoperla inermis Kaćanski & Zwick, 1970					x	x	x	x									x	x	x	x				
Isoperla cf. *lugens* (Klapálek, 1923)				x	x	x	x	x									x	x	x	x				
Isoperla oxylepis (Despax, 1936)				x	x												x	x	x					
Isoperla rivulorum (Pictet, 1841)																	x	x						
Isoperla non det.						x	x	x										x	x	x				
Perlodes cf. *intricatus* Pictet, 1841																	x	x	x					
Perlodes non det.					x	x	x																	
Total	0	0	6	19	18	12	6	7	6	6	1	0	0	3	14	16	21	12	7	7	6	7	3	0

recorded in habitats with a moderate water temperature (<18°C) (Graf *et al*., 2009, 2017), our data indicates that it tolerates even higher values (*e.g*. measured here a maximum of 22.9°C).

Even though the proportion of each functional feeding group varied between study sites, the assemblages mainly consisted of shredders, gatherers and grazers, which reflects differences in the availability of food resources (Vannote *et al*., 1980). The dominance of shredders at the headwaters of upper lotic habitats is in accordance with the River Continuum Concept (Vannote *et al*., 1980), as these habitats are under the strong influence of surrounding vegetation and the high input of coarse particulate organic matter (CPOM). While the Crna rijeka River spring is shaded by surrounding vegetation, at the open canopy Bijela rijeka River spring macrophytes are main source of CPOM (Ivković *et al*., 2015). Tufa barriers are natural lake outlets, containing trapped organic matter transported from the upstream towards the downstream lakes (Miliša *et al.,* 2006; Špoljar *et al*., 2007). Therefore, as expected, these stonefly assemblages were dominated by gatherers-collectors. Overall, the observed decreasing abundance of shredders and grazers and the increasing abundance of gatherers-collectors from upstream to downstream sites is in accordance with the overall predictions of the River Continuum Concept (Vannote *et al*., 1980). Similar results were obtained for caddisfly assemblages in the same hydrosystem (*i.e.* upstream sites were dominated by shredders, and tufa barriers by collectors), due to the specificity of these habitats and available food resources (Previšić *et al*., 2007; Šemnički *et al*., 2012).

Feeding strategies and food availability are closely related to the microhabitat selection (Graf *et al*., 2009), and some of the species showed a significant preference for a specific microhabitat type. The preferences of *P. praecox* and *P. intricata* for microhabitats with mosses were in accordance with previous studies (Graf *et al.,* 2009, 2017; Krno *et al*., 2015). However, the same microhabitat preferences represent a discrepancy for *A. triangularis* which usually favours microhabitats with an inorganic substrate (*i.e.* micro- and mesolithal, psammal and argyllal). Our results showed that microhabitats with mosses are associated with the highest current velocity. Stonefly larvae can use mosses as a refugee from predators as well as a food resource. The water current supplies the microhabitat with a particulate organic matter, which is being retained on the mosses (Habdija *et al*., 2004; Miliša *et al*., 2006). Higher amounts of trapped organic matter on mosses therefore provided a more desirable microhabitat for the rheophilous gatherers-collectors *A. triangularis* and *P. intricata* (Graf *et al*., 2009, 2017) due to the more substantial food resources in an otherwise oligotrophic hydrosystem (Špoljar *et al*., 2007). The rheophilous *P. praecox* is predominantly a shredder although it was also recorded as feeding on POM (Graf *et al*., 2009). Stonefly shredders were already documented as the dominant moss inhabitants, in some cases even feeding on moss leaves (Mutch and Pritchard, 1984; Glime, 2017). The moss leaves and the trapped organic matter on these leaves could thus have provided the species with adequate food resources.

Stonefly emergence patterns and abundance

Stonefly emergence mainly occurred between February and November, and contrary to our expectations, for the majority of species it followed typical Central European patterns (Graf *et al.,* 2009, 2017; Zwick, 2011). As headwaters are generally thermally stable habitats, photoperiod most probably triggered the initiation of the emergence periods at these sites (Ivković *et al*., 2015). On the contrary, downstream at sites, water temperature was the key-factor, corroborating previous studies (Illies, 1971; Hynes, 1976; Zwick, 2011; Ivković *et al*., 2015; Vilenica *et al*., 2017a). This was particularly obvious at tufa barriers, where the emergence was more seasonal compared to other habitats, due to the highest oscillations in water temperature. In some taxa, such as in a majority from the Perlodidae family, emergence began earlier in 2007, which is related to higher water temperatures during the spring of 2007 compared to the spring of 2008. Higher water temperatures were already recorded as causing an earlier start in emergence (Illies, 1971; Harper and Peckarsky, 2006; Zwick, 2011). Several long-term studies have shown that discharge patterns are one of the most important factors influencing changes in aquatic insect assemblages between years (Wagner and Schmidt, 2011; Ivković *et al*., 2012, 2014; Vilenica *et al*., 2017a). Differences in stonefly abundances between the two studied years could therefore be related to a higher discharge in 2008 which caused a more prominent downstream larval drift (Sertić Perić *et al*., 2011), resulting in a lower number of emerging adults. However, a lower number of individuals emerged in 2007 from the Korana River, as the river dried out during the summer of 2007, while it was perennial in 2008. Additionally, these differences could also be attributed to the high abundance of the rheophilous *P. intricata* in 2008. A higher number of individuals also emerged in 2008 from the Bijela rijeka River, primarily dominated by *P. auberti*, which has already been observed to have higher population abundances during periods of higher discharge (Ivković *et al*., 2013). Higher discharge is associated with a higher water velocity, which brings more nutrients into the habitat (Allan, 1995). The higher amounts of organic matter trapped at tufa barrier Kozjak-Milanovac could thus have favoured one of the shredders/gatherers-collectors, *N. cinerea*, resulting in the dominance of this species in 2008 and the generally higher abundance of emergent individuals.

In agreement with available literature data, stonefly life cycles were primarily univoltine (Graf *et al*., 2009, 2017; Zwick, 2011), while several species showed indications of plurivoltinism. Flexible life cycles were previously recorded for *N. pictetii* and *L. nigra* (Hildrew *et al.,* 1980; Elliott, 1987; Lillehammer *et al*., 1989; Wolf and Zwick, 1989; Nesterovitch and Zwick, 2003; Graf *et al*., 2009, 2017; Zwick, 2011), while the non-typical bimodal emergence of *L. albida* in 2007 could be attributed to favourable environmental conditions (*e.g.* small temperature oscillations) or to cohort splitting caused by an acceleration of growth of some larvae (Giller and Malmqvist, 1998; Nesterovitch and Zwick, 2003; Zwick, 2011). Following Central European data (Zwick, 2011), the longest emergence period was recorded for *P. auberti*, the species that inhabits springs and adjacent spring runs where it opportunistically exploits the optimal temperature conditions (Zwick, 2011).

CONCLUSIONS

Karst systems have been poorly studied as lotic habitats for stoneflies. Our study clearly demonstrates that knowledge of ecological traits of European stoneflies is incomplete and therefore provides novel information on their ecological traits. We have found that in this karst system in the Plitvice Lakes National Park favourable environmental conditions exist to support highly diverse stonefly assemblages. The composition and structure of these assemblages are primarily determined by the position of the habitat within the system which affects water temperature, pH, dissolved oxygen, and nutrient and energy sources. Observed phenological traits within this southern European karst system are comparable to Central European ones: the majority of the recorded species were univoltine and emerged during spring. Our results provide additional insight to the knowledge of stonefly emergence patterns and ecological preferences and could be used to improve future conservation and nature resource management of European freshwater habitats.

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